



RO-4-125

Changing distribution patterns of an endangered butterfly: Linking local extinction patterns and variable habitat relationships

Kristine L. Preston^{a,d,*}, Richard A. Redak^{a,b}, Michael F. Allen^{a,c}, John T. Rotenberry^{a,c}

^a Center for Conservation Biology, University of California, Riverside, CA 92521, USA

^b Department of Entomology, University of California, Riverside, CA 92521, USA

^c Department of Biology, University of California, Riverside, CA 92521, USA

^d Nature Reserve of Orange County, 15600 Sand Canyon Avenue, Irvine, CA 92618, USA

ARTICLE INFO

Article history:

Received 11 September 2011

Received in revised form 2 March 2012

Accepted 11 March 2012

Keywords:

Agricultural intensification

Euphydryas editha quino

Extinction

Grazing

Precipitation

Urbanization

ABSTRACT

Multiple processes are increasingly recognized as being responsible for species' extinctions. We evaluated population extinctions between 1930 and 1998 for the endangered Quino checkerspot (*Euphydryas editha quino*) butterfly relative to agricultural history, human population growth, climate variability, topographical diversity, and wildflower abundance. Overall agricultural land use was calculated for extinct and extant populations based upon cultivation and grazing intensities averaged across five time periods reflecting distinct agricultural practices from 1769 to present. Extinct populations were associated with a history of more intensive agriculture and greater human population growth at time of extinction. A long history of intensive livestock grazing was the strongest agricultural predictor of extinction. Based upon historic vegetation maps, extinct butterfly populations were typically isolated from other known populations by 1930, and in landscapes fragmented by cultivation and development. Precipitation and topographical variability were not important predictors of extinction. Wildflower host plants and nectar sources have declined across the butterfly's range because of invasive plants and habitat loss. The proportion of years considered average or abundant in wildflowers declined significantly during extinction periods. The Quino checkerspot has shifted in distribution from the coast into foothills and mountains. Newly discovered higher elevation populations experience more precipitation and are buffered from drought. Efforts to conserve Quino checkerspot are enhanced by understanding that the butterfly's decline and shifting distribution is a complex multi-scale process related to agricultural history, human population growth, climate variability, and wildflower decline.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Multiple interacting stressors are driving species to extinction (Brook et al., 2008). Butterflies are especially sensitive to environmental change and accelerating extinction rates are leading to a global decline in butterfly diversity (Forister et al., 2010; Potts et al., 2010; Warren and Bourn, 2010). These declines are associated with urban and agricultural expansion and changing agricultural practices (Maes and Van Dyck, 2001; Stefanescu et al., 2004; Norris et al., 2010; Warren and Bourn, 2010; Fattorini, 2011). Agricultural intensification employing large-scale cultivation and use of pesticides and herbicides is reducing butterfly diversity (Schmitt and Rákossy, 2007; Marini et al., 2009; Ekroos et al., 2010; Warren and Bourn, 2010). Livestock grazing also

affects butterfly populations, although the nature of the relationship depends on butterfly life history traits, plant community succession, grazing regimes, and invasive plant dynamics (Swengel, 2001; Pöyry et al., 2005; Schtickzelle et al., 2007; Vogel et al., 2007). In some species, lack of grazing leads to population extinction, whereas in others over-grazing causes extinction. Invasive species are another threat to butterfly populations (Moroñ et al., 2009; Potts et al., 2010; Wagner and Van Driesche, 2010).

Climate change may cause future large-scale extinctions and interact with other drivers to accelerate extinction and biodiversity loss (Purvis et al., 2000; Brook et al., 2008). Insects are especially vulnerable to global warming as ambient temperature controls body temperature influencing metabolic reaction rates and life history phenology (Parmesan, 2006; Memmott et al., 2007; Wilson and Maclean, 2011). Precipitation patterns are changing with extremes in precipitation increasing (Easterling et al., 2000; IPCC, 2007; Seager et al., 2007). Increasing climate variability can lead to phenological mismatches between butterflies and host plants

* Corresponding author at: Center for Conservation Biology, University of California, Riverside, CA 92521, USA. Tel.: +1 951 827 2621; fax: +1 951 827 2620.
E-mail address: Kristine.Preston@ucr.edu (K.L. Preston).

causing population extinctions (Ehrlich et al., 1980; McLaughlin et al., 2002; Parmesan, 2006; Hegland et al., 2009; Singer and Parmesan, 2010).

To effectively conserve declining species, it is important to understand the multiple processes leading to extinction. The endangered Quino checkerspot butterfly (*Euphydryas editha quino*) provides an opportunity to evaluate the association between population extinction and global change processes, including changing climate and land use. Quino checkerspot is the southernmost subspecies of Edith's checkerspot (*E. editha*), which is broadly distributed throughout western North America. The range of Edith's checkerspot has shifted northward and upwards in elevation, consistent with global warming predictions (Parmesan, 1996). Quino checkerspot populations exhibited the highest extinction rates, as expected for southerly populations in a warming and drying climate. Currently, this butterfly may be undergoing a range shift into higher elevations (USFWS, 2009), consistent with climate change predictions for the species (Parmesan, 1996; Preston et al., 2008). However, local extinctions and changes in historic distribution are also attributed to extensive habitat loss and degradation resulting from urban and agricultural land uses (Mattoni et al., 1997; USFWS, 1997, 2003).

In this paper, we evaluate spatial and temporal patterns of extinction in southern California populations of Quino checkerspot relative to agricultural history, human population growth, climate and topographic variability, and wildflower abundance. We also assess distributional changes and differences in environmental conditions across the United States (US) portion of the subspecies' historic and current range. Insights derived from these analyses will help us understand those environmental conditions under which Quino checkerspot populations may be more resilient or susceptible to global change processes. Such knowledge is important in prioritizing lands for conservation and informing management of this endangered subspecies.

2. Methods

2.1. Study system

Quino checkerspot was formerly distributed throughout cis-montane southern California, US and northern Baja California, Mexico. Our southern California study area extends from the Pacific Ocean east through valleys, foothills, and mountains to the desert edge (Fig. 1). Climate, vegetation, and topography vary substantially. This once widespread and abundant butterfly currently occupies open coastal sage scrub and chaparral shrublands with native forbs. In early studies, Quino checkerspot primarily used *Plantago erecta* as a larval host plant with secondary use of *Plantago ovata* (Singer, 1971, 1982; White, 1974). More recently, butterflies have been observed using other host plants, particularly at higher elevation sites. These include *Castilleja exserta*, *Plantago patagonica*, *Antirrhinum coulterianum*, *Collinsia concolor*, and *Cordylanthus rigidus* (Mattoni et al., 1997; Pratt and Pierce, 2008; USFWS, 2003, 2009). Adult Quino checkerspot use multiple nectar sources, including species in the *Cryptantha*, *Eriodictyon*, *Gilia*, *Lasthenia*, *Lomatium*, *Muilla*, and *Plagiobothrys* genera. More than 75% of the butterfly's former range has been converted to agriculture and urban development, prompting listing as a federally-endangered species in 1997 (USFWS, 1997).

Quino checkerspot likely have a complex metapopulation structure with large (20–100 fold) fluctuations over 10–20 year periods (Mattoni et al., 1997; USFWS, 2009). Under certain environmental conditions, Quino checkerspot populations can explode in size and defoliate larval host plants leading to massive dispersal events (Murphy and White, 1984; White and Levin, 1981). Large

populations tend to persist in more extensive, diverse habitats, whereas smaller, lower quality habitats are temporarily colonized by butterflies following massive dispersal events and sufficient rainfall for larval host plant growth. Extirpation of large, source populations is likely to lead to long term extinction in an area. In Edith's checkerspot, the annual timing and amount of precipitation drives population fluctuations by determining larval survival; 99% of pre-diapause larvae can die from starvation when host plants senesce after winter rains (Ehrlich et al., 1980).

2.2. Temporal and spatial patterns of the butterfly's distribution

To assess the spatial and temporal distribution of Quino checkerspot occurrences in the study area, we combined current butterfly locations with historic records and mapped observations by decade.

2.3. Environmental databases for modeling

To compare land use and climate differences at extinct and extant Quino checkerspot populations, we developed a database characterizing agricultural history, human population size, and precipitation and topographical variability. These data were derived from many sources and linked spatially to each population (Appendix Table 1). We developed a second environmental dataset using Geographic Information Systems (GISs) software and digital data to calculate variables reflecting current environmental conditions across the historic and present range of Quino checkerspot.

2.3.1. Environmental conditions at extinct and extant butterfly populations

For our analysis of environmental factors associated with extinction, we identified extinct populations and selected comparable extant populations for the purposes of calculating environmental variables during equivalent time periods. Extant populations were undeveloped locations where Quino checkerspot have been recorded since 1998. Extinct populations were those where a butterfly was detected historically (1905–1982) but has not been recorded since 1998. We defined the extinction period as the 20-year window centered on the last recorded butterfly observation. This period corresponds to the 10–20 year cycle in which butterfly populations can fluctuate exponentially and during which environmental conditions likely influence population dynamics leading to extinction (Mattoni et al., 1997; USFWS, 2003, 2009).

We calculated environmental variables during relevant time periods for each extinct population and then selected the closest extant population to calculate environmental variables during the same time periods. If there were no nearby extant populations, we selected an extant population in similar proximity to the coast as the extinct population. The intent was to select extinct and extant populations comparable in environmental conditions so that factors most strongly associated with extinction could be distinguished.

2.3.1.1. Human population. We used the size of the human population near a Quino checkerspot population as a proxy for the relative amount of historic habitat loss to urbanization (Forister et al., 2010). We used 1930 Wieslander Vegetation Type Maps (VTMs) to assess the level of development versus natural habitat in the vicinity of each butterfly population prior to the period of documented population extinctions (Wieslander, 1935; VTM, 2011). We aggregated decadal US Census Bureau human population data for counties, cities, and towns (Forstall, 1995; CSDF, 2000) in the vicinity of Quino checkerspot populations. We defined "vicinity" as a distance of ≤ 5 km between the butterfly population and a town or city, which is within Quino checkerspot's dispersal

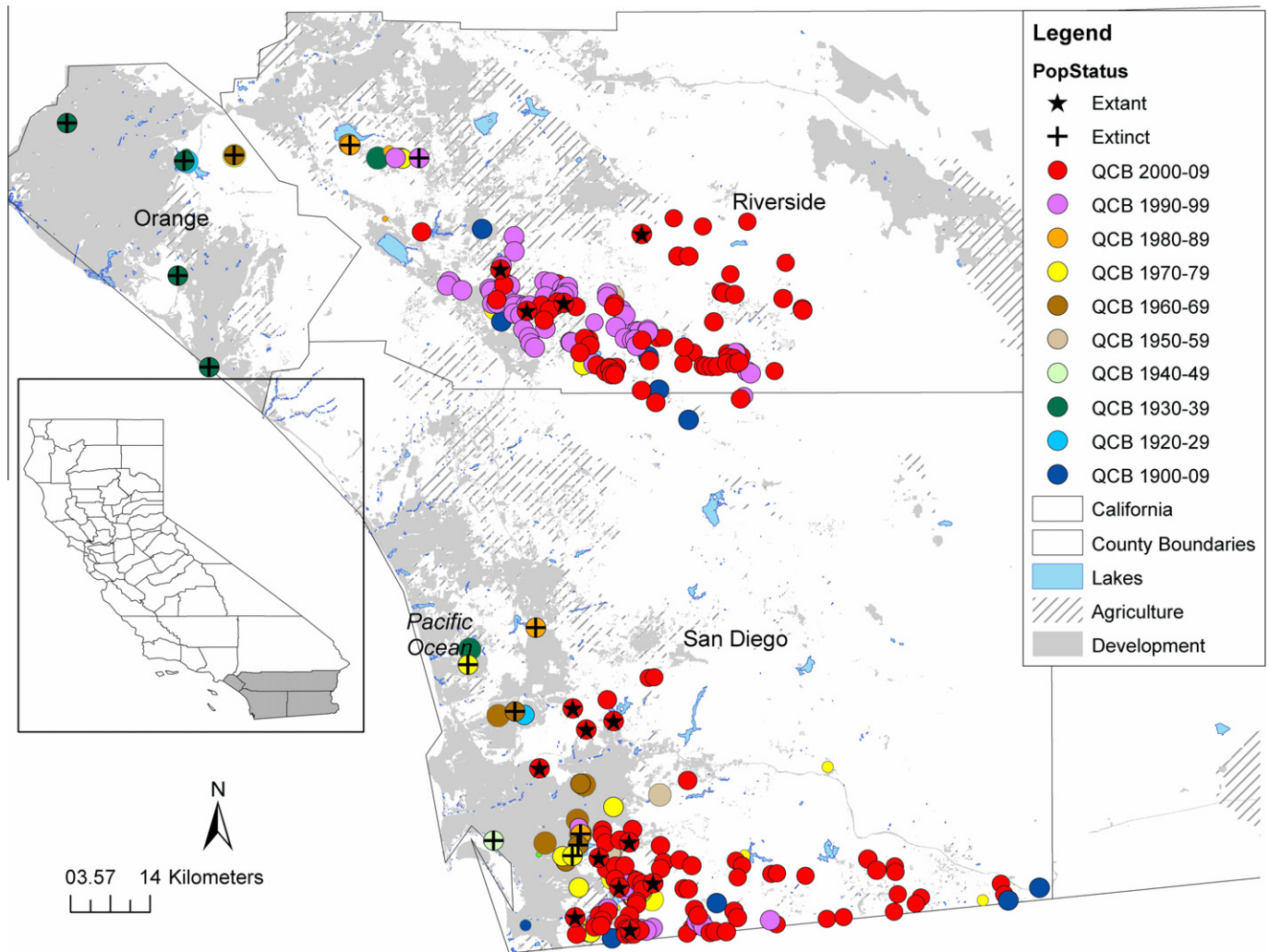


Fig. 1. Quino checkerspot butterfly (QCB) study area and butterfly locations classified by colored circles according to the most recent decade in which an observation was reported. Also shown are locations of extinct (triangle) and extant (circle) populations used in modeling.

capabilities (Harrison, 1989; Parmesan, 1996). We used maps with jurisdictional boundaries (Rand McNally, 2004, 2008) and a GIS layer of cities (ESRI, 2005) to determine towns and cities ≤ 5 km from butterfly populations. Growth in human population was calculated as the difference in population density between the decade prior to the last butterfly observation for an extinct population and the decade following that observation. Human population growth was calculated for the same time period for the comparable extant population.

2.3.1.2. Agricultural history. To categorize land use change associated with agricultural practices, a score was developed for each population reflecting the relative intensity of grazing and cultivation over five discrete time periods between 1769 and present. These time periods represent different patterns of agricultural production in this region (Johnston and McCalla, 2004). Agriculture was introduced into California by Spanish missionaries in 1769. During the Spanish Mission/early Mexican (1769–1834) and Mexican rancho (1835–1848) periods, livestock grazing was the predominant form of agriculture. The early California statehood period (1849–1889) is characterized by cattle production, with a switch in the 1870s to sheep production and dry farming of wheat and barley. The agricultural intensification period (1890–1930) includes expansion of dry farming and rapid growth of intensive irrigated crops, such as fruits and vegetables. After 1930, there was

further growth of agriculture, although following World War II a population boom converted large areas of farmland to urban/suburban development.

We compiled historical records from many sources (Appendix Table 1) to estimate relative livestock grazing intensities ≤ 5 km from extinct and extant Quino checkerspot populations. We used historic Wieslander Vegetation Type Maps (VTMs) to assess spatial patterns of agriculture and natural vegetation near butterfly populations in 1930 (Wieslander, 1935; VTM, 2011). Lands used for livestock grazing were assigned a grazing intensity score based upon categories of livestock stocking rates (number of hectares/head of cattle/horse; Appendix Table 2). Cut-offs for stocking rates within each grazing category were based upon historic livestock grazing intensities in California (Minnich, 2008). Extinct and extant butterfly populations were given numeric scores for each time period based upon average livestock production records or upon typical stocking rates for that area. We used descriptions of historic land use (Appendix Table 1) to identify whether there was significant livestock grazing near populations or whether land was used for farming, urban/suburban development or left undisturbed. We categorized intensity of livestock grazing before 1930 to reflect grazing history before extinction and after 1890 to represent the period before and during extinction episodes. We also quantified grazing for only the decades prior to (1890–1930) and during (post-1930) documented butterfly extinctions.

In a similar manner, we compiled cultivation information from different sources (Appendix Table 1). We scored each extinct and extant population for relative intensity of cultivation during the five time periods (Appendix Table 2). We used historic Wieslander VTMs to categorize the amount of cultivated land ≤ 5 km of butterfly populations in 1930, the start of the period of extinctions examined in this study. Cultivation included dry farming (grains) and irrigated crops (orchards, vineyards, vegetables, and hay). We calculated cultivation intensity from 1890 through 1930 to reflect conditions preceding extinctions and after 1930 to characterize extinction episodes.

To quantify overall agricultural land use for each population, we calculated an average score representing combined grazing and cultivation scores across the five time periods.

2.3.1.3. Climate. We obtained weather station records closest to extinct and extant Quino checkerspot populations and calculated climate parameters (WRCC, 2012). Since precipitation and temperature are highly correlated, we focused on precipitation variables, which are important in Edith's checkerspot population dynamics (Ehrlich et al., 1980; McLaughlin et al., 2002). We calculated mean and standard deviation annual rainfall (August 1–July 31) for the entire weather station record and for the 20-year extinction period at each population. Extremely low precipitation years experienced less precipitation than one standard deviation below the mean precipitation for the butterfly population with the lowest average rainfall. Similarly, extremely high precipitation years were those receiving more precipitation than one standard deviation above the mean precipitation of the population with the highest average rainfall. Thresholds defining extreme rainfall years were ≤ 140 mm and ≥ 566 mm of precipitation.

We summarized precipitation from December to June of the rainfall year, the period of time most relevant to the Quino checkerspot life-cycle. We determined the proportion of extreme rainfall years for the entire weather station record for each population. For each extinct population, we calculated the difference between the proportion of extreme December to June rainfall years for the 20 year extinction window and preceding years of the weather station record. We also calculated this for the comparable extant population during the same time period. To further assess whether extreme precipitation was associated with extinction, we conducted a two sample paired *t*-test with extinct populations testing the null hypothesis that the proportion of extreme precipitation years was higher during the extinction period than in preceding years. We conducted the same analysis for extant populations.

2.3.1.4. Topography. Topography plays a strong role in sister subspecies Bay checkerspot (*E. editha bayensis*) larval development and survival and the timing of adult emergence (Weiss et al., 1988, 1993). We used a vector ruggedness measure (VRM) calculated in GIS to quantify local variation in terrain, this measure is less dependent on slope than other methods (Sappington et al., 2007). Vector analysis is used with a raster-based digital elevation model to decompose each grid cell into x, y, and z components using trigonometry and the slope and aspect of the cell. We calculated terrain ruggedness for a 3×3 neighborhood of 90 m cells at each population location.

2.3.1.5. Wildflower abundance. Minnich (2008) compiled newspaper records categorizing annual wildflower abundance for Los Angeles County from 1886 to 2007 and Riverside County from 1918 to 2007. Orange County was originally part of Los Angeles County and was included in the analysis. We had no wildflower records for San Diego County. For each extinct population in Los Angeles, Orange and Riverside counties, we calculated the proportion of years that wildflowers were average or high in abundance

during the extinction period. We then calculated the proportion of average and high wildflower years for the period prior to extinction. We used a two sample paired *t*-test to test the null hypothesis that for extinct populations, wildflower abundance was lower during the extinction period than the preceding period.

2.3.2. GIS-based environmental dataset to compare butterfly habitats

For a larger-scale analysis of habitat relationships across the current distribution of Quino checkerspot, we used ARCGIS 9.1 software (ESRI, 2005) to calculate environmental variables from various digital source layers for a 1 km^2 grid across the study area. For each Quino checkerspot location we extracted values for environmental variables at the grid cell encompassing the location. Climate variables included average annual precipitation and minimum January temperature (OSU, 2006). To characterize topography we used a 90-m resolution Digital Elevation Model (USGS, 2006) to calculate median values for elevation, slope, and aspect within a 1 km^2 cell. Land cover variables included percent of coastal sage scrub and chaparral habitats and agricultural and developed lands within 1 km^2 , as calculated from a vegetation map for the region (CDF, 2006).

2.4. Modeling methods

2.4.1. Model construction

2.4.1.1. Comparing extinct versus extant populations. We constructed and compared alternative logistic regression models to distinguish between environmental conditions associated with extinct versus extant populations. These models represented different *a priori* hypotheses regarding the importance of land use and climate in association with population extinction. We used an information-theoretic comparative approach to evaluate alternative models (Burnham and Anderson, 2002).

2.4.1.1.1. Butterfly extinctions, agriculture, human population, precipitation and terrain ruggedness. To explore the relationship of local-scale butterfly extinctions and land use change, climate variability, and topographic heterogeneity, we developed models comparing average intensity of agriculture (grazing and cultivation) since 1769 with human population growth, the difference in proportion of extreme precipitation during December through June rainfall years before and during the extinction period, and terrain ruggedness. We created a global model incorporating all four variables and alternative models with land use versus climate/topographic variables and interaction terms. We avoided multicollinearity by examining correlations among pairs of variables and for $r > 0.7$ we retained only one of the independent variables in the model (Tabachnick and Fidell, 1996).

2.4.1.1.2. Butterfly extinctions, grazing, and cultivation intensity over different time periods. We ran a second series of models to explore the association between butterfly population extinction and livestock grazing and crop cultivation during different time periods. We calculated intensity of grazing and cultivation, for the entire period preceding extinction (1769–1930) and several decades prior (1890–1930), during extinction (post-1930), and for the entire history of agriculture from 1769.

2.4.1.2. Environmental conditions across the Quino checkerspot's distribution. To determine if there were environmental differences within the current distribution of Quino checkerspot populations, we characterized environmental attributes for locations where Quino checkerspot populations were historically documented and still persist with areas where populations have only recently been detected. “Established” populations included both historical (<1998) and current locations, whereas “newly discovered” included a distinct region with no spatially explicit location records before 1998. We calculated mean \pm standard deviation values for

environmental variables. We used the comparative logistic regression modeling approach to evaluate differences in climate, vegetation, and land use at established versus newly discovered locations. As there were more records for established populations, we randomly selected a subset of these records to obtain equivalent sample sizes for modeling.

2.4.2. Model evaluation

To select the best approximating model(s), we used Akaike's information criterion adjusted for small samples (AIC; Burnham and Anderson, 2002). We selected the model with the lowest AIC_c value and calculated a difference in AIC_c (Δ_i) for each model. We computed Akaike weights (ω_i) representing the probability that a model was the best approximating model for the dataset. We also calculated an evidence ratio representing the probability that the model with the highest ω_i was likely to be correct compared to another model. Based upon cumulative Akaike weights, we identified a $\geq 95\%$ confidence subset of best approximating models. To evaluate the relative importance of each variable, we calculated model averaged parameter estimates (MAPEs) and cumulative variables weights (CVWs).

3. Results

3.1. Temporal and spatial patterns of the Quino checkerspot's distribution

Quino checkerspot butterflies were historically recorded from the coast to the foothills of southern California (Fig. 1). Between the 1930s and 1970s the butterfly disappeared from most coastal areas. Current populations are distributed in the central and eastern portions of the butterfly's historic range. Most recent observations are clustered in southwestern Riverside County, particularly in the foothills, and in southern San Diego County. The most easterly distributed newly discovered locations in Riverside County were first documented in 1998 and are at higher elevations in the Peninsular Mountains.

3.1.1. Patterns of extinction relative to 1930 land use

Inspection of the VTMs reveals that in 1930 southern California was largely agrarian with human population centers in the major cities of Los Angeles, Riverside, and San Diego. There was extensive cultivation along the coast in northern Orange and San Diego counties and in large interior valleys. Native shrublands along the coast were fragmented by grassland, cultivated fields, and rural residences. Extensive native shrublands, particularly chaparral, were located away from the coast at higher elevations in the Santa Ana Mountains and Peninsular foothills. Only a few areas with large expanses of potential habitat lack historic butterfly observations, such as foothills/mountains in southern Orange County and northern San Diego County. In 1930 only 18% of butterfly populations that later went extinct had shrublands encompassing more than 50% of the area within 5 km of their location, compared with 58% of extant populations. Extinct populations were also more isolated in 1930, with only 9% having a known butterfly population within 5 km compared with 92% of extant populations.

3.2. Environmental conditions at extinct versus extant populations

We classified 14 local Quino checkerspot populations as extinct and selected 14 comparable extant populations within the historically established range (Fig. 1).

3.2.1. Butterfly extinctions, agriculture, human population, and precipitation

In distinguishing between extinct and extant Quino checkerspot populations three candidate models comprised a 97% confidence subset of best approximating models (Table 1). The top-ranked model included average agricultural intensity since 1769 and growth in human population during the extinction period. All three candidate models included these two variables. Difference in proportion of extreme precipitation years during the extinction period, terrain ruggedness, and interaction between agricultural intensity and human population growth did not improve performance of the other two candidate models.

There was a positive relationship between extinction and average agricultural intensity (Fig. 2a; MAPE: 0.10; 90% C.I.: 0.01–0.18). Agricultural intensity was an important predictor of extinction (CVW = 0.99). Extinct populations showed variable levels of human population growth (Fig. 2b), but there was a positive association between human population growth and extinction (MAPE: 0.0001; 95% C.I.: 0.0000–0.0003). Human population growth was as important as agriculture in predicting extinction (CVW of 0.97). Average annual rainfall (Fig. 2c) and minimum January temperature did not differ between extinct and extant populations. The difference in proportion of extreme December to June rainfall years during the 20-year extinction window compared with previous years did not show a trend relative to extinction (Fig. 2d, MAPE: 0.07; 95% C.I.: –0.07 to 0.21). Terrain ruggedness also did not show a trend in association with extinction (Fig. 2e, MAPE: –0.14; 95% C.I.: –0.37 to 0.09). CVWs of 0.42 indicate extreme precipitation and terrain ruggedness were substantially less important than land use in distinguishing between extinct and extant butterfly populations.

There was a subtle difference in extreme precipitation for extinct and extant populations that was detected only with paired sample comparisons. For extinct populations, the proportion of extreme rainfall years was significantly higher during the extinction period (mean \pm standard deviation: 0.10 ± 0.06) compared with the prior period (0.06 ± 0.06 ; Paired two-sample *t* test, $t = 2.49$, $p = 0.01$). Similarly, for extant populations extreme rainfall was greater in the extinction period (0.13 ± 0.06) compared with the prior period (0.08 ± 0.05 ; Paired two-sample *t* test, $t = 2.50$, $p = 0.01$).

3.2.2. Butterfly extinctions, grazing, and cultivation

Three models comprised a 98% confidence subset of models relating livestock grazing and cultivation intensities over different time periods to butterfly extinction (Appendix Table 3). Average grazing intensity from 1769 to 1930 was the most important predictor of extinction. The best approximating model with a weight of 0.75 included only pre-1930 grazing, which had a positive association with extinction (Fig. 2f; MAPE: 1.36; 95% C.I.: 0.14–2.58; CVW = 0.98).

The second ranked model included pre-1930 grazing and post-1930 cultivation ($\Delta_i = 2.74$; $\omega_i = 0.19$; $\omega_i/\omega_1 = 3.9$), while the third ranked model included these two variables and an interaction term ($\Delta_i = 5.66$; $\omega_i = 0.05$; $\omega_i/\omega_1 = 13.8$). Post-1930 cultivation intensity showed no trend in relation to extinction (Fig. 2g; MAPE: 0.01; 95% C.I.: –0.13 to 0.15; CVW = 0.24). Other measures of grazing and cultivation were unimportant predictors of extinction.

3.2.3. Butterfly extinctions and wildflower abundance

Based upon newspaper accounts (Minnich, 2008), thirteen extinct Quino checkerspot populations in Los Angeles, Orange, and Riverside Counties had significantly fewer average or high abundance wildflower years (mean \pm standard deviation: 0.18 ± 0.16 ; Paired two-sample *t*-test, $t = -5.795$, $p < .0001$) during the extinction period than prior to extinction (0.51 ± 0.16). Between 1886 and 1918, 73% of years with records in Los Angeles County were classified as average or high abundance wildflower years. However,

Table 1

Performance of logistic regression models^a in distinguishing between extinct and extant populations of Quino checkerspot relative to human population, precipitation extremes, terrain ruggedness and cumulative agricultural land use scores from first European settlement to present. K represents the number of model parameters, Δ_i is the difference in AIC_c values for each model relative to the model with the lowest AIC_c, ω_i is the model weight, and ω_i/ω_1 is the evidence ratio.

Model parameters	K	Δ_i	ω_i	ω_i/ω_1
Agriculture and human population	4	0.000	0.444	
Agriculture, human population, terrain ruggedness and December–June extreme precipitation	6	0.147	0.413	1.1
Agriculture, human population and interaction	5	2.796	0.110	4.0
Agriculture	3	6.353	0.019	23.9
Terrain ruggedness	4	8.256	0.007	61.7
Human population	3	9.614	0.004	123.3
Terrain ruggedness and December–June extreme precipitation	5	10.508	0.002	191.4
Terrain ruggedness, December–June extreme precipitation and interaction	5	13.09	0.001	191.4
December–January extreme precipitation	3	13.686	0.001	888.0

^a Models highlighted in bold form 96% confidence subset of best approximating models. Variables are defined in the methods.

between 1918 and 2007, only 9% of years were average with no high abundance years. This trend in declining wildflower populations proceeded inland with increasing low abundance years beginning in the 1940s in Riverside County. However, wildflower fields have persisted in areas of western Riverside County with high abundances recorded as late as 1952 and average abundances as late as 2003. Populations remaining extant during the period of wildflower decline are located in eastern portions of the butterfly's range where wildflowers have remained more abundant.

3.3. Environmental variation across the historic and current range

In characterizing differences in environmental attributes across the historic range of Quino checkerspot, the butterfly's current distribution is shifted toward higher elevations (Fig. 3a). This is caused by the extinction of low elevation coastal populations and occurrence of newly discovered populations in the Peninsular Mountains. These latter populations receive substantially more rainfall than extinct or established populations (Fig. 3b). The proportion of extreme rainfall years calculated from long-term weather station records varies by region and tends to be lower for newly discovered populations (Fig. 3c). Average minimum January Temperature between 1970 and 2000 was much lower for newly discovered populations (Fig. 3d). There was little difference in the amount of current urban and agricultural development for established populations (Fig. 3e and f). Newly discovered populations occur in landscapes with more chaparral and less coastal sage scrub (Fig. 3g and h).

3.3.1. Environmental conditions at established versus newly discovered populations

Three logistic regression models formed a 95% confidence subset in distinguishing between established and newly discovered populations and all three models included climate variables (Table 2). The single most important predictor was annual rainfall with a CVW of 1.0; annual rainfall was lower at established populations (MAPE: –0.11; 95% C.I.: –0.18 to –0.03). The proportion of extreme rainfall years at weather stations near populations did not show a trend (MAPE: 2.70; 95% C.I.: –25.75 to 31.16; CVW = 0.35). Minimum January temperature was highly correlated with precipitation ($r = -0.96$, $p < .0001$) and was not used in modeling. Land use and vegetation variables showed no trends in distinguishing between established and newly discovered populations and CVWs were less than 0.10.

4. Discussion

4.1. Environmental conditions at extinct versus extant populations

Quino checkerspot population extinctions in southern California were most strongly associated with agricultural inten-

sity from 1769 to present and to human population growth during the extinction period. By the early 1930s agriculture and rural development had led to extensive habitat loss and fragmentation. Climate played a subtle and localized role; it was not an important predictor of extinction, although extinct populations had significantly more extreme rainfall years during the extinction period. Climate variability may have exacerbated the effects of habitat loss and degradation on Quino checkerspot population dynamics. An interaction between habitat loss, degradation, and climate variability contributed to Bay checkerspot population extinctions where extreme precipitation was associated with large population fluctuations (Ehrlich et al., 1980; McLaughlin et al., 2002). Habitat loss and degradation resulted in the inability of butterflies to recolonize isolated habitat patches after populations were extirpated as a result of climate variability.

Many Quino checkerspot populations in southern California likely disappeared prior to the extinction events examined in this study (Mattoni et al., 1997). The Wieslander VTMs indicate that by 1930 populations that went extinct over the next six decades occurred in relatively isolated natural habitats fragmented by agriculture. Temporal and spatial patterns of Quino checkerspot population extinctions mirror trends in agricultural intensity and human population growth. Thus, land use practices may have directly caused butterfly extinctions through habitat destruction as well as indirectly through loss of resilience. Fragmented habitats with butterfly extinction following stochastic events (e.g., fire, flood, drought) would likely remain unoccupied because of isolation from other butterfly populations.

4.1.1. Butterfly extinctions, grazing, invasive plants, and declining wildflowers

Quino checkerspot population extinctions were associated with a longer, more intensive history of grazing. Those areas with the longest history of grazing and highest livestock stocking rates comprised the best pasture (Minnich, 2008) and were where butterflies initially went extinct. Other studies have also documented relationships between livestock grazing, quantified at relatively coarse scales, and landscape-scale patterns of butterfly diversity, abundance, population dynamics, and extinction (Hoyle and James, 2005; Pöyry et al., 2005; Saarinen and Jantunen, 2005).

The causal relationship between livestock grazing and Quino checkerspot population extinction is unknown. Grazing can cause direct mortality of immobile larvae and pupae through trampling (Weiss, 1999; Swengel, 2001; Schtickzelle et al., 2007). Grazing can indirectly affect butterflies by reducing the richness and abundance of native larval host and nectar plants and by altering vegetation structure and microclimate, thereby impacting thermoregulatory environments for developing larvae (Swengel, 2001; Hoyle and James, 2005; Saarinen and Jantunen, 2005; Schtickzelle et al., 2007). It is conceivable that over-grazing led to Quino checkerspot population extinctions in the 1800s when stocking rates

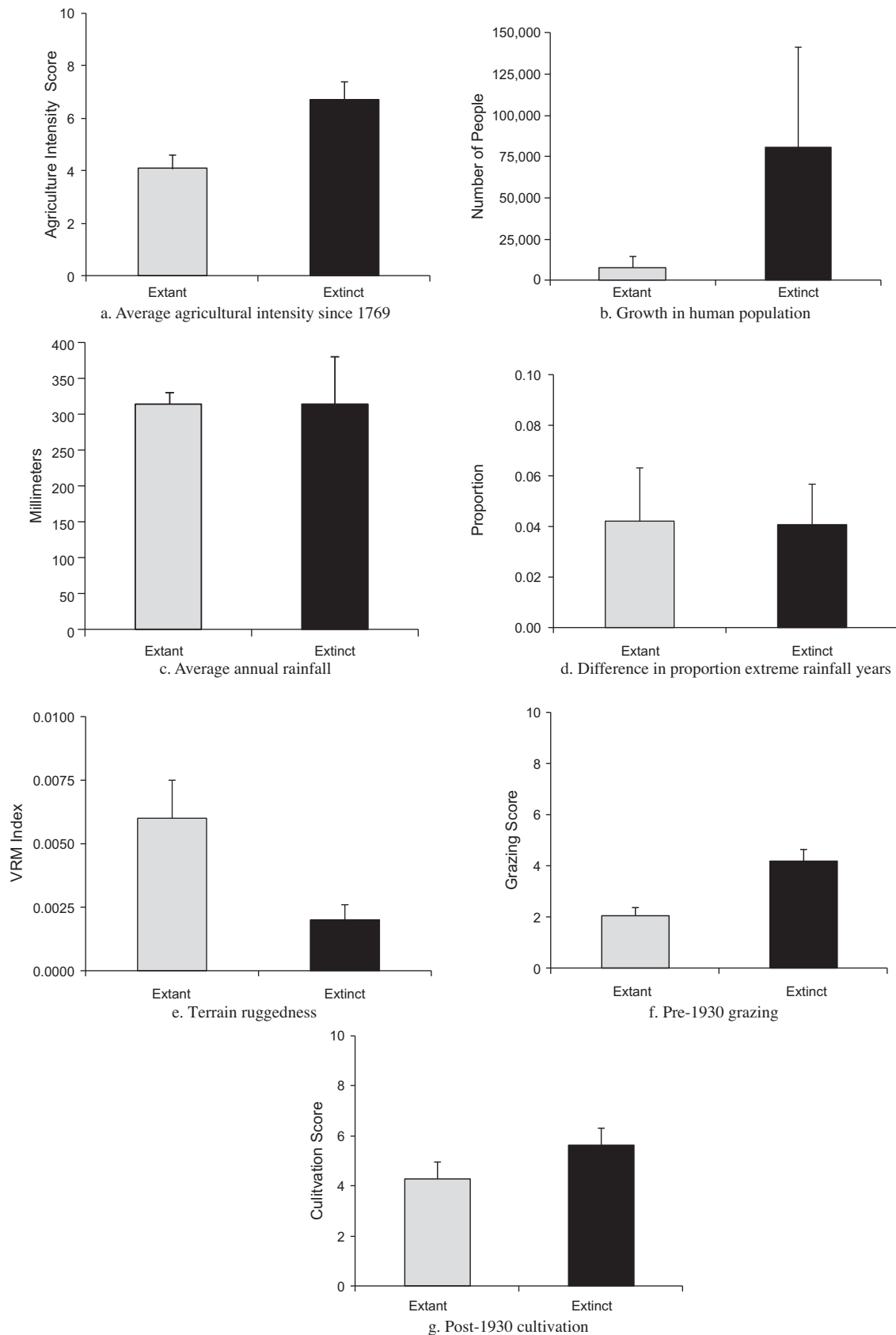


Fig. 2. Environmental attributes at 14 extinct and 14 extant Quino checkerspot populations.

were at their highest and that populations remaining in the 1930s were remnants of a previously more abundant distribution.

Based upon descriptions of Spanish Explorers, missionaries, and early settlers, the best pasture lands supported diverse and

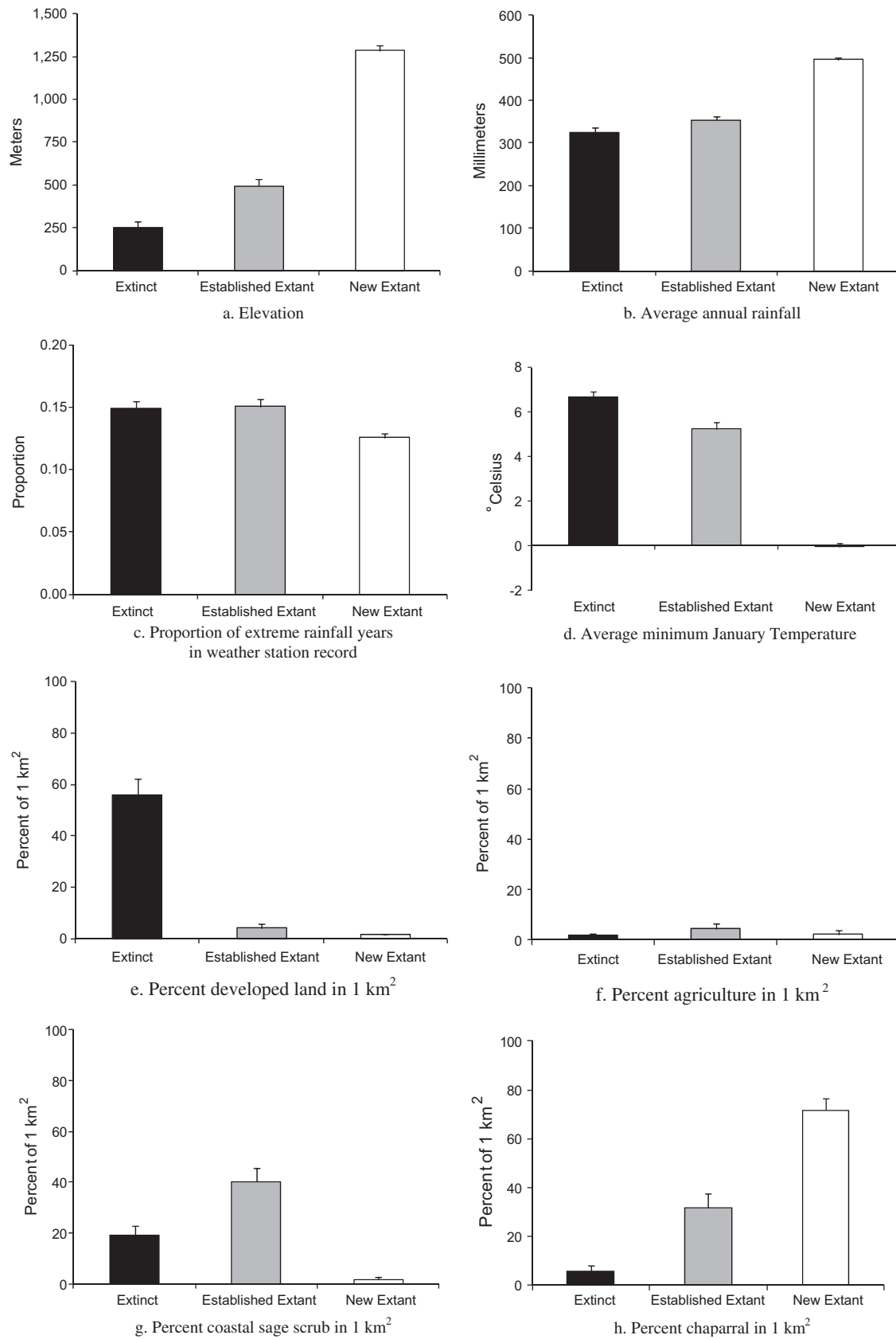


Fig. 3. Environmental attributes at regions currently occupied by Quino checkerspot compared with regions where the butterfly is extinct. “Extinct” indicates areas with no butterfly records since 1998, “established extant” indicates currently occupied areas where the butterfly was historically documented, and “new extant” indicates areas with no location records prior to 1998.

Table 2

Performance of logistic regression models^a in distinguishing between newly discovered and established extant Quino checkerspot populations relative to current land use (percent agriculture and development in 1 km²) and natural (climate, percent vegetation in 1 km²) environmental factors. K represents the number of model parameters, Δ_i is the difference in AIC_c values for each model relative to the model with the lowest AIC_c, ω_i is the model weight, and ω_i/ω_1 is the evidence ratio.

Model type	Model parameters	K	Δ_i	ω_i	ω_i/ω_1
Climate	Annual rainfall	3	0.000	0.654	
Climate	Annual rainfall, proportion extreme rainfall	4	2.044	0.235	2.8
Climate and land use	Annual rainfall, proportion extreme rainfall, % agriculture, % development	6	4.638	0.064	10.2
Climate and vegetation	Annual rainfall, proportion extreme rainfall, % chaparral, % coastal sage scrub	6	5.834	0.035	18.5
Climate, vegetation and land use	Annual rainfall, proportion extreme rainfall, % chaparral, % coastal sage scrub, % agriculture, % development	8	8.257	0.011	62.3
Vegetation	% Coastal sage scrub	3	48.451	0.000	6540000000.0
Vegetation	% Chaparral, % coastal	4	50.514	0.000	>6540000000.0
Vegetation and land use	% Chaparral, % coastal sage scrub, % agriculture, % development	6	54.084	0.000	>6540000000.0
Vegetation	% Chaparral	3	71.341	0.000	>6540000000.0
Climate	Proportion extreme rainfall	3	81.394	0.000	>6540000000.0
Land use	% Development	3	90.508	0.000	>6540000000.0
Land use	% Agriculture	3	92.007	0.000	>6540000000.0
Land use	% Agriculture, % development	4	92.027	0.000	>6540000000.0

^a Models highlighted in bold form 95% confidence subset of best approximating models. Variables are defined in the methods.

abundant wildflower communities. These areas were also where exotic Mediterranean plants were first introduced and established (Mattoni et al., 1997; Minnich, 2008). Open forb lands with patches of shrubs are characteristic of high quality Quino checkerspot habitat. As late as the early 1900s, primary host and nectar plants for this butterfly were still common. However, southern California wildflowers started a precipitous decline in abundance around 1920 (Minnich, 2008). The trend in decreasing wildflower abundance began at the coast and spread inland, although in some years wildflowers are still average abundance in Riverside County, especially in areas with poor soils. The pattern and timing of wildflower decline corresponds with patterns of Quino checkerspot population extinctions.

Invasive annual grasses in combination with urban development and agricultural expansion contributed to the collapse of extensive native wildflower fields (Minnich, 2008). A suite of Mediterranean annual grasses first invaded coastal areas in the late 1800s, became well established by the 1930s, and then expanded into inland valleys (Wieslander, 1935; Minnich, 2008). This wave of invaders included red brome (*Bromus rubens*), ripgut brome (*Bromus diandrus*), and slender wild oat (*Avena barbata*). The rapid decline of Quino checkerspot in the 20th century is likely caused in part by invasive plants and the collapse of native wildflower fields. Invasive grasses reduce the abundance of native larval host and nectar plants and bare ground available for optimal larval development (Weiss, 1999; Osborne and Redak, 2000). Invasive annual grasses have also contributed to population extinctions in other Edith's checkerspot subspecies (Weiss, 1999; Severns and Warren, 2008).

Intensive grazing can facilitate invasion of exotic plants and likely played a role in the spread and dominance of exotic grasses in California's native plant communities (Leiva et al., 1997; Weiss, 1999; Hayes and Holl, 2003; Seabloom et al., 2003; HilleRisLambers et al., 2010). Although livestock grazing may have contributed to the spread of invasive grasses and forbs, it can also be used to control these species and aid in the return of native species. Butterfly species, including the Bay checkerspot, have benefited from low intensity, managed grazing that reduces exotic grass cover and increases nectar and larval host plant cover (Weiss, 1999; Pöyry et al., 2005; Vogel et al., 2007; Thomas et al., 2010). Intensity and duration of livestock grazing, in relation to other factors determines the magnitude and type of impact grazing has on butterfly populations.

4.1.2. Extinction and cultivation intensity

Cultivation intensity and crop types varied across the study area. There was no clear association between cultivation intensity

and extinction. Cultivation was localized and of low intensity from 1769 until the late 1800s. By 1930, the most intensively cultivated areas were coastal plains and river valleys with access to water for irrigating crops. Inland areas were used for dry farming barley and wheat. Extinct Quino checkerspot populations were located near irrigated orchards and crops, whereas extant populations near cultivation tended to be in dry farming regions.

4.1.3. Extinction and human population growth

Human population growth was associated with extinction; although, there was considerable variability. A number of extinctions occurred when the surrounding human population was relatively small. Human population was used as an indicator of urbanization driving habitat loss and fragmentation; we assumed that the larger the population the greater the area impacted by urban activities. This measure is an approximation of impacts and does not provide an actual overlay of converted land relative to butterfly populations. It also underestimates the impact of rural and semi-rural development. It is clear that urban development has fundamentally changed the southern California landscape and areas in which butterfly populations have gone extinct in Orange and San Diego counties currently support substantially higher levels of development compared with extant populations.

4.2. Historic distribution or range shift in response to changing climate?

Parmesan (1996) documented a northward and upward elevation shift in the overall range of Edith's checkerspot associated with changing climate. While habitat degradation and isolation could increase extinction rates, these factors were not thought to contribute to the latitudinal range shift in Edith's checkerspot. Quino checkerspot has not demonstrated a northward shift; rather, extant populations are occurring at higher elevations as predicted by climate change modeling (Parmesan, 1996; Preston et al., 2008). Quino checkerspot populations may have historically occurred, but were unrecorded, at higher elevations along their eastern range margin. High elevation populations are not unprecedented, as populations of Edith's checkerspot occur in the Sierra Nevada and San Bernardino Mountains (Thomas et al., 1996; Mattoni et al., 1997).

Alternatively, newly discovered populations may represent a range shift in response to changing climate, as these high elevation areas are buffered against drought compared with established areas within the historic distribution. Future climate projections for southern California predict temperatures will increase;

precipitation may decrease and is expected to be more variable, with longer, more severe droughts and more intense floods (Seager et al., 2007). The eastern edge of Quino checkerspot's range supports large and robust butterfly populations, abundant and diverse larval host plants and nectar sources, and relatively low levels of development and intensive agriculture. These areas may provide climate refugia that Quino checkerspot will require under future predicted scenarios of climate change (Preston et al., 2008).

5. Conclusion

Local-scale extinctions of Quino checkerspot butterfly populations in southern California were related to agricultural history, human population growth, and wildflower decline. The association of extreme precipitation with extinction was outweighed by the effects of land use. Butterfly population extinctions coincided with spatial and temporal patterns of habitat loss, high intensity grazing, invasion by exotic annual grasses, and wildflower decline. At a larger scale, differences within the distribution of extant Quino checkerspot populations were best predicted by climate variables. Higher elevation populations are buffered from drought. To develop conservation plans and management actions that result in successful long-term conservation of Quino checkerspot, it is important to recognize that multiple stressors operating at different scales influence population dynamics and changes in the butterfly's distribution.

Acknowledgements

Financial support was provided by the Center for Conservation Biology and Department of Entomology at the University of California, Riverside, the California State Department of Transportation, Waste Management, and the Shipley Skinner Reserve-Riverside County Endowment. The US Fish and Wildlife Service, Riverside County Regional Conservation Authority, and T. Scott supplied butterfly location data used in modeling. A. Anderson, E. Porter, and colleagues at the US Fish and Wildlife Service provided insight into historic and current butterfly distributions. R. Johnson, A. Hinojosa, C. Gonzalez-Abraham, and M. Davis provided Geographic Information Systems assistance. V. Rorive provided critical administrative support.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2012.03.011>.

References

- Brook, B.W., Sodhi, N.S., Bradshaw, C.J.A., 2008. Synergies among extinction drivers under global change. *Trends Ecol. Evol.* 23, 453–460.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, second ed. Springer-Verlag, New York.
- CDP (California Department of Forestry and Fire Protection), 2006. Digital Vegetation Map. <http://frap.cdf.ca.gov/projects/frap_veg/> (accessed 03.08.06).
- CSDF (California State Department of Finance), 2000. Historical Census Populations of Places, Towns, and Cities in California, 1850–2000. <<http://www.dof.ca.gov/research/demographic/reports/census-survey>> (accessed 28.05.10).
- Easterling, D.R., Meehl, J., Parmesan, C., Chagnong, S., Karl, T.R., Mearns, L.O., 2000. Climate extremes: observations, modeling and impacts. *Science* 289, 2068–2074.
- Ehrlich, P.R., Murphy, D.D., Singer, M.C., Sherwood, C.B., White, R.R., Brown, I.L., 1980. Extinction, reduction, stability and increase: the response of checkerspot butterfly (*Euphydryas*) populations to California drought. *Oecologia* 46, 101–105.
- Ekroos, J., Heliölä, J., Kuussaari, M., 2010. Homogenization of lepidopteran communities in intensively cultivated agriculture landscapes. *J. Appl. Ecol.* 47, 459–467.
- ESRI, 2005. ArcGIS Desktop 9.1 Service Pack 1. Redlands.
- Fattorini, S., 2011. Insect extinction by urbanization: a long term study in Rome. *Biol. Conserv.* 144, 370–375.
- Forister, M.L., McCall, A.C., Sanders, N.J., Fordyce, J.A., Thorne, J.H., O'Brien, J., Waetjen, D.P., Shapiro, A.M., 2010. Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. In: *Proceedings of National Academy of Sciences*. <www.pnas.org/cgi/doi/10.1073/pnas.0909686107>.
- Forstall, R.L., 1995. Population of Counties by Decennial Census: 1900 to 1990. <<http://www.census.gov/population/cencounts/ca190090.txt>>.
- Harrison, S., 1989. Long-distance dispersal and colonization in the Bay checkerspot butterfly, *Euphydryas editha bayensis*. *Ecology* 70, 1236–1243.
- Hayes, G.F., Holl, K.D., 2003. Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. *Conserv. Biol.* 17, 1694–1702.
- Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A., Totland, Ø., 2009. How does climate warming affect plant–pollinator interactions? *Ecol. Lett.* 12, 184–195.
- HilleRisLambers, J., Yelenik, S.G., Colman, B.P., Levine, J.M., 2010. California annual grass invaders: the drivers or passengers of change? *J. Ecol.* 98, 1147–1156.
- Hoyle, M., James, M., 2005. Global warming, human population pressure, and viability of the world's smallest butterfly. *Conserv. Biol.* 19, 1113–1124.
- IPCC, 2007. *Climate Change 2007: The Physical Science Basis, Summary for Policy-makers. Contributions of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Geneva, Switzerland. <<http://www.ipcc.ch>>.
- Johnston, W.E., McCalla, A.F., 2004. Whither California Agriculture: Up, Down or Out? Some Thoughts about the Future. Giannini Foundation Special Report 04–1. University of California Agriculture and Natural Resources.
- Leiva, M.J., Chapin III, F.S., Ales, R.F., 1997. Differences in species composition and diversity among Mediterranean grasslands with different history – the case of California and Spain. *Ecography* 20, 97–106.
- Maes, D., Van Dyck, H., 2001. Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario? *Biol. Conserv.* 99, 263–276.
- Marini, L., Fontana, P., Klimek, S., Battist, A., Gaston, K.J., 2009. Impact of farm size and topography on plant and insect diversity of managed grasslands in the Alps. *Biol. Conserv.* 142, 394–403.
- Mattoni, R., Pratt, G.F., Longcore, T.R., Emmel, J.F., George, J.N., 1997. The endangered Quino checkerspot, *Euphydryas editha quino* (Lepidoptera: Nymphalidae). *J. Res. Lepidoptera* 34, 99–118.
- McLaughlin, J.F., Hellman, J.J., Boggs, C.L., Ehrlich, P.R., 2002. Climate change hastens population extinctions. *Proc. Natl. Acad. Sci.* 99, 6070–6074.
- Memmott, J., Craze, P.G., Waser, N.M., Price, M.V., 2007. Global warming and the disruption of plant–pollinator interactions. *Ecol. Lett.* 10, 710–717.
- Minnich, R.A., 2008. *California's Fading Wildflowers: Lost Legacy and Biological Invasions*. University of California Press, Berkeley.
- Moroñ, E., Lenda, M., Skórka, P., Szentgyörgyi, J., Settele, J., 2009. Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscapes. *Biol. Conserv.* 142, 1322–1332.
- Murphy, D.D., White, R.R., 1984. Rainfall, resources, and dispersal in southern populations of *Euphydryas editha* (Lepidoptera: Nymphalidae). *Pan-Pacific Entomol.* 60, 350–354.
- Norris, K., Asase, A., Collen, B., Cockowski, J., Mason, J., Phalan, B., Wade, A., 2010. Biodiversity in a forest-agriculture mosaic – the changing face of West African rainforests. *Biol. Conserv.* 143, 2341–2350.
- Osborne, K.H., Redak, R.A., 2000. Microhabitat conditions associated with the distribution of postdiapause larvae of *Euphydryas editha quino* (Lepidoptera: Nymphalidae). *Ann. Entomol. Soc. Am.* 93, 110–114.
- OSU (Oregon State University), 2006. PRISM Digital Temperature and Precipitation Data. <<http://www.prism.oregonstate.edu/>> (accessed March 2006).
- Parmesan, C., 1996. Climate and species' range. *Nature* 382, 765–766.
- Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. *Ann. Rev. Ecol. Syst.* 37, 637–639.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353.
- Pöyry, J., Lindgren, S., Salminen, J., Kuussaari, M., 2005. Responses of butterfly and moth species to restored cattle grazing in semi-natural grasslands. *Biol. Conserv.* 122, 465–478.
- Pratt, G.F., Pierce, C.L., 2008. A new larval host plant, *Collinsia concolor*, for the endangered Quino checkerspot, *Euphydryas editha quino*. *J. Lepidopterists Soc.* 64, 36–37.
- Preston, K.L., Rotenberry, J.T., Redak, R., Allen, M.F., 2008. Habitat shifts of endangered species under altered climate conditions: importance of biotic interactions. *Glob. Change Biol.* 14, 2501–2515.
- Purvis, A., Jones, K.E., Mace, G.M., 2000. Extinction. *BioEssays* 22, 1123–1133.
- Rand McNally, 2004. *The Thomas Guide: Riverside and San Diego Counties Street Guide*. Chicago.
- Rand McNally, 2008. *The Thomas Guide: Orange County Street Guide*. Chicago.
- Saari, K., Jantunen, J., 2005. Grassland butterfly fauna under traditional animal husbandry: contrasts in diversity in mown meadows and grazed pastures. *Biodivers. Conserv.* 14, 3201–3213.
- Sappington, J.M., Longshore, K.M., Thompson, D.B., 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mohave Desert. *J. Wildlife Manage.* 71, 1419–1426.
- Schmitt, T., Rákossy, L., 2007. Changes of traditional agrarian landscapes and their conservation implications: a case study of butterflies in Romania. *Divers. Distrib.* 13, 855–862.

- Schtickzelle, N., Turlure, C., Baguette, M., 2007. Grazing management impacts on the viability of the threatened bog fritillary butterfly *Proclossiana eunomia*. *Biol. Conserv.* 136, 651–660.
- Seabloom, E.W., Harpole, W.S., Reichman, O.J., Tilman, D., 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proc. Natl. Acad. Sci.* 100, 13384–13389.
- Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H., Harnik, N., Leetmaa, A., Lau, N., Li, C., Velez, J., Naik, N., 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316, 1181–1184.
- Severns, P.M., Warren, A.D., 2008. Selectively eliminating and conserving exotic plants to save an endangered butterfly from local extinction. *Anim. Conserv.* 11, 476–483.
- Singer, M.C., 1971. Evolution of food-plant preference in the butterfly *Euphydryas editha*. *Evolution* 25, 383–389.
- Singer, M.C., 1982. Quantification of host preference by manipulation of oviposition behavior in the butterfly *Euphydryas editha*. *Oecologia* 52, 224–229.
- Singer, M.C., Parmesan, C., 2010. Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philos. Trans. Roy. Soc. Biol.* 365, 3161–3176.
- Stefanescu, C., Herrando, S., Páramo, F., 2004. Butterfly species richness in the north-west Mediterranean Basin: the role of natural and human-induced factors. *J. Biogeogr.* 31, 905–915.
- Swengel, A.B., 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodivers. Conserv.* 10, 1141–1169.
- Tabachnick, B.G., Fidell, L.S., 1996. *Using Multivariate Statistics*, third ed. HarperCollins College Publishers, New York.
- Thomas, C.D., Singer, M.C., Boughton, D.A., 1996. Catastrophic extinction of population sources in a butterfly metapopulation. *Am. Nat.* 148, 957–975.
- Thomas, J.A., Simcox, D.J., Clarke, R.T., 2010. Successful conservation of a threatened *Maculinea* butterfly. *Science* 325, 80–83.
- USFWS (US Fish and Wildlife Service), 1997. Endangered and threatened wildlife and plants: determination of endangered status for the laguna mountain skipper and Quino checkerspot butterfly. *Federal Register* 62, 2313–2322.
- USFWS (US Fish and Wildlife Service), 2003. Recovery Plan for the Quino Checkerspot Butterfly (*Euphydryas editha quino*). Portland.
- USFWS (US Fish and Wildlife Service), 2009. 50 CFR part 17 endangered and threatened wildlife and plants; revised designation of critical habitat for the Quino checkerspot butterfly (*Euphydryas editha quino*); final rule. *Federal Register* 74, 28775–28862.
- USGS (United States Geological Survey), 2006. Digital Elevation Model. <<http://seamless.usgs.gov/>> (accessed March 2006).
- Vogel, J.A., Debinski, D.M., Koford, R.R., Miller, J.R., 2007. Butterfly responses to prairie restoration through fire and grazing. *Biol. Conserv.* 140, 78–90.
- VTM, 2011. Wieslander Vegetation Type Mapping, College of Natural Resources, Geospatial Imaging and Informatics Facility, UC, Berkeley. <<http://vtm.berkeley.edu>> (accessed 14.05.11).
- Wagner, D.L., Van Driesche, R.G., 2010. Threats posed to rare or endangered insects by invasions of nonnative species. *Ann. Rev. Entomol.* 55, 547–568.
- Warren, M.S., Bourn, N.A.D., 2010. Ten challenges for 2010 and beyond to conserve Lepidoptera in Europe. *J. Insect Conserv.* 15, 321–326.
- Weiss, S.B., Murphy, D.D., White, R.R., 1988. Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. *Ecology* 69, 1486–1496.
- Weiss, S.B., Murphy, D.D., Ehrlich, P.R., Metzler, C.F., 1993. Adult emergence phenology in checkerspot butterflies: the effects of macroclimate, topoclimate, and population history. *Oecologia* 96, 261–270.
- Weiss, S.B., 1999. Cars, cows, and checkerspot butterflies: nitrogen deposition and management of nutrient-poor grasslands for a threatened species. *Conserv. Biol.* 13, 1476–1486.
- White, R.R., 1974. Food plant defoliation and larval starvation of *Euphydryas editha*. *Oecologia* 14, 307–315.
- White, R.R., Levin, M.P., 1981. Temporal variation in vagility: implications for evolutionary studies. *Am. Midl. Nat.* 105, 348–357.
- Wieslander, A.E., 1935. A vegetation type map of California. *Madroño* 3, 140–144.
- Wilson, R.J., Maclean, I.M.D., 2011. Recent evidence for the climate change threat to Lepidoptera and other insects. *J. Insect Conserv.* 15, 259–268.
- WRCC, 2012. Western Regional Climate Center Climate Data. <<http://www.wrcc.dri.edu>> (accessed February 2012).